

CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS

VII. SOME PTERIDOSPERM STEMS FROM IOWA

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The occurrence of richly fossiliferous coal balls in the Upper Pennsylvanian rocks of Iowa has been reported by Darrah in 1939 and 1941. In the latter paper he gives a list of the species observed as well as a brief discussion of the dominant floral elements. The distribution and occasional abundance of these petrifications in Iowa is now sufficiently well known so as to render a detailed review unnecessary, but certain introductory remarks are in order relative to the general floristics, as compared with the Illinois coal balls.

In September, 1944, Mr. Frederick O. Thompson of Des Moines very generously turned over to the writer, for study and preservation in the Henry Shaw School of Botany, a selected portion of his remaining coal-ball specimens. All of this material was collected from the highly prolific, although now abandoned, Urbandale mine located on the north side of U. S. Highway No. 6, 1.2 miles west of the city limits (63rd Street) of Des Moines. The coal seam from which the petrifications were obtained lies 185 feet below the surface, the elevation of the latter being 805 feet. It is regretted that a more precise stratigraphical position, other than "the Des Moines Series," cannot be given at this time. The author has been informed that a detailed study of the stratigraphy of this region will be published shortly, and it is hoped that this information may be given in the next number of our "Contributions" which will deal with seeds from the Urbandale coal balls.

Our collection consists of approximately 110 cut slabs which vary from 3 to 20 cm. in diameter. It is admittedly small as coal ball collections are accounted, yet rich in the number of seeds, leaves, pteridosperm stems, fertile fern-like foliage, and other plant parts, many of which are either striking novelties or very imperfectly known.

During the three years prior to the war the paleobotanical work in this laboratory was devoted very largely to a study of fossil plants from certain southern Illinois mines.¹ Although the progress made in that region constitutes but little more than a bare introduction to the field work lying ahead, it does seem clear that the Carboniferous flora that occupied much of southern Illinois was dominantly pteridophytic. Certainly the Herrin coal from the great Pyramid strip mine south of Pinckneyville was formed to a very considerable extent from the remains of *Lepidodendron* (Pannell, '42), and the roof shales above the same coal in the

¹ See parts I-VI of this "Contributions" series, in *Ann. Mo. Bot. Gard.* 29-30. 1942-43.
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Old Ben mine #11, in Franklin County, display a preponderance of arborescent lycopods, articulates, and ferns.

Lepidodendron is so preponderant in the Pyramid mine coal balls that we have on numerous occasions all but decided to abandon further collecting there, yet the constant lure of fragments of other plants has brought us back time and again, and it is very probable that this will continue for some time.²

It seems reasonably safe to express the opinion that the study of coal balls is a phase of paleobotany that promises to be long and productive. It is only in England that anything approaching exhaustive studies has been carried on, and even there we have no reason to assume that the task is completed. The works of Williamson and Scott, and a number of other British paleobotanists of Scott's period, were based on coal-ball petrifications, yet few of these investigators were collectors. If we may judge from Scott's written works and his magnificent slide collection, his source of supply was primarily through the medium of professional collectors and other persons. Thus only the more striking and obviously new things reached his hands. Perhaps it would be asking too much to expect one man to contribute more, yet I cannot help but feel that Scott's contributions would have had an even more vital effect on the following generation had he personally supervised the cutting of some few tons of coal balls in his own laboratory.

Judging from our own experience in Illinois and from Mr. Thompson's vast collections, most of which are deposited at Harvard University, it seems clear that large-scale collecting is the primary requisite to the restoration of reasonably complete plants and their assemblage into correspondingly complete paleo-landscapes. Studies of the flora of an individual coal ball are certainly a thing of the past. Productive mines must be revisited many times and collections considered in terms of tons. This may savor of mass production rather than "scientific procedure," yet it is the only way in which scattered parts of the plants may be brought together and those plants assembled into representative restorations.

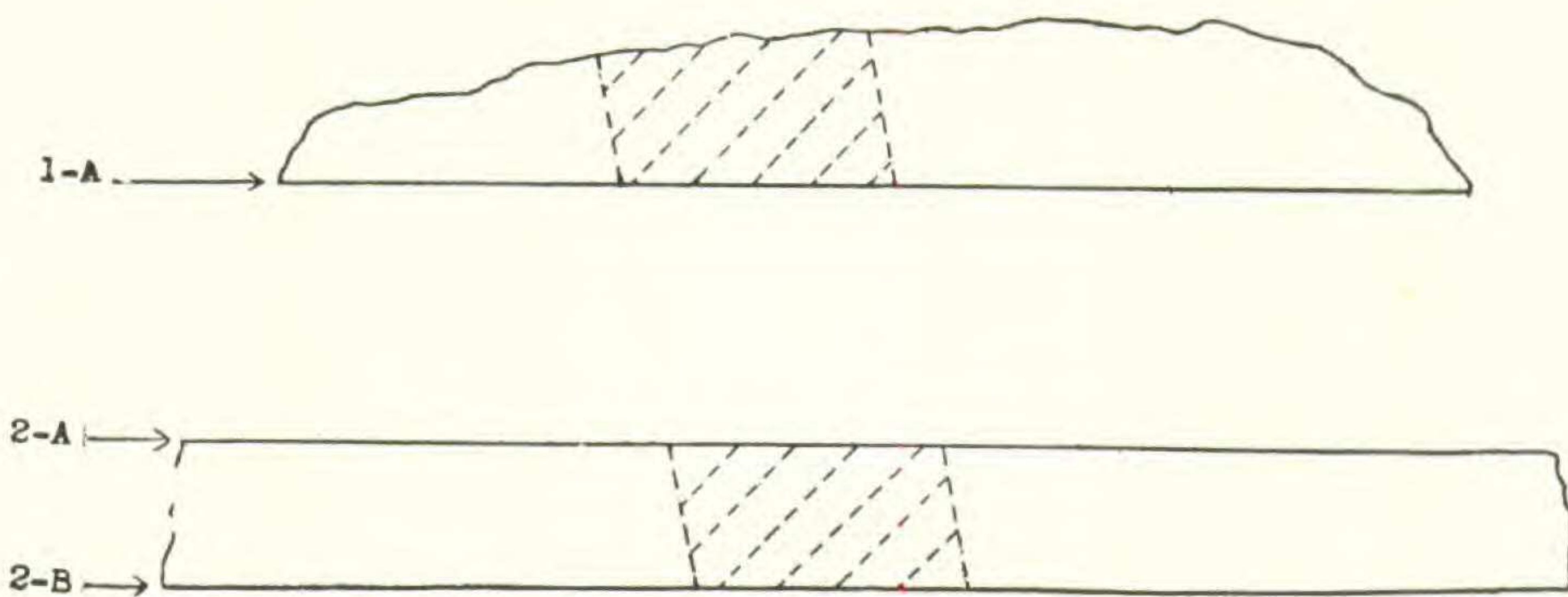
To return to the Pyramid coal balls, evidence of seed plants in the petrifications from that mine are meager indeed. Apparently they were not abundant in the immediate environs, and the Urbandale specimens from Des Moines thus present a most striking contrast. Although fern-like fructifications are present in some abundance the Lycopods are comparatively rare, their place being taken by an extensive array of seeds, Cordaitan stems and leaves, and stem-remains seemingly referable to the Pteridospermeae. From this assemblage the latter have been selected for primary consideration.

***Medullosa Thompsonii* sp. nov.**

The following description of this stem is based on two slices cut from a coal ball approximately 15 cm. in diameter, one being an end cut. Both are approximately 1.5 cm. thick, and the stem passes through both pieces. Between these two

² In a collection of coal balls obtained from the Pyramid mine in December, 1944, one contains numerous specimens of *Cordaianthus* which is, judging from a preliminary study, closely related to *C. Sbuleri* Darrah. In view of the frequent occurrence of *Mesoxylon* it is not surprising that *Cordaianthus* should have turned up, although this is the first record of it from that region so far as I am aware.

portions of the original coal ball, one or two slices, apparently totaling a little more than 3 cm. in thickness, have been removed. Mr. Thompson, the collector, has informed me that this intermediate portion was one of the specimens sent to the Botanical Museum at Harvard University some few years ago which have not been available for study. There is, however, no doubt as to the relationship between the two pieces in our collection.



Text-fig. 1. Sectional view through coal ball WCB420, with approximate position of *Medullosa Thompsonii* stem shown in shaded area; 1-A represents face A of block 1, and 2-A, 2-B represent faces A and B of block 2. Reduced about one-half.

Aside from its other significant features, this stem (and the remains of other Medullosan stems, petioles, roots and leaflets in associated coal balls) is of special interest in that it demonstrates stelar fusions more clearly than has been reported in any previously described species of the Anglorota (Schopf, '39) group. Text-fig. 1 shows the order in which the preparations were made.

The Stem and Leaf Bases.—

The stem measures approximately 4.3 x 3.0 cm., exclusive of the petiole base shown at the left in fig. 1. It is slightly crushed and must have been cylindrical, or nearly so, measuring about 3.6 cm. in diameter in life. It consists of three sharply defined regions: an outer fibrous cortex (rind) which certainly contributed appreciably to the support of the plant, a broad inner parenchymatous cortex, and a central stelar system bounded externally by a band of periderm. Every section also displays the bases of at least one or two petioles in various stages of departure. It is possible to distinguish sharply between petiole base and stem only where the rind is in the process of developing between the two. Thus in fig. 1 the partitioning fibrous tissue is shown developing at point *a*, preparatory to the departure of the petiole at the left.

Those who are familiar with the Medullosas will observe an unmistakable similarity between this stem and the English *M. anglica*. A number of differences will be pointed out in the course of the description which, it is believed, adequately justify the distinct specific designation.

The rind is bounded by an epidermis consisting of brick-shaped cells slightly elongated radially (fig. 32). The radial, and especially the outer walls, are somewhat thicker than the inner ones. This is probably accounted for, in part, by the former presence of a cuticle, although it has not been possible to distinguish this from the wall of the epidermal cells.

The cortical cells, which are small and nearly isodiametric immediately within the epidermis, gradually increase in size, attaining a maximum within the fibrous zone. In *Medullosa anglica* the outermost cortical layer is illustrated (Scott, '99, fig. 13) as being palisade-like after the fashion of the epidermis. No such differentiation of the outer cortex is present in the Iowa specimen. In cross-section the fibrous strands (fig. 5) are circular to slightly elongate radially. These anastomose, although only at very extended intervals, and appear in longitudinal section as very nearly parallel strands. An especially noteworthy feature of this part of the stem lies in the rarity of associated secretory canals. They are present deeper within the cortex although markedly less conspicuous than in *M. anglica* and other related species.

It may be noted that in fig. 1, from approximately points *b* to *c*, the fibrous strands are lacking. The rind is replaced in this region by a periderm (fig. 33) consisting of an outer uniform layer of phellem 4 to 5 cells deep; within this there is a somewhat broader band of phelloderm of less regularly aligned cells which merge with the larger cells of the cortex within; and in between these two tissues lies what apparently was the phellogen. These terms are used as they are conventionally applied to living plants on the assumption that they correspond to the respective tissues of a normal periderm. In his description of *M. anglica*, Scott mentions a similar "distinct interruption of the hypoderma cortical fibers between the bases of adjacent leaves," and he suggested that it was in this region that the adventitious roots were inserted. While it is not possible to confirm this with *M. Thompsonii* it seems very likely that such may have been the case. Although Medullosan roots are abundant in other associated coal balls none were found in organic connection with the stem. This might be explained by the fact that our specimen probably represents a fragment of the plant from some distance above the ground.

The internal or stelar periderm differs in no way from that of other related species. At the level of the stem represented by surface A of block 2 it encloses three steles, lettered *x*, *y*, and *z* in fig. 2. The ground tissue immediately surrounding the steles is not sufficiently well preserved to merit further consideration. The steles vary with respect to size and development of secondary xylem. Stele *x* measures approximately 7.0 x 3.5 mm. and is somewhat crushed; stele *y* is 2.0 mm.; and stele *z* is 6.0 x 3.0 mm. in diameter.

Like the periderm, the primary wood seems to present no characters of special distinction. The secondary wood, however, is notably endocentric, being (Schopf, '39, p. 203) weakly developed towards the outside (fig. 2). Although the relative arrangement of the three steles has been slightly distorted, the position they

occupy in block 1, where all three are fused together (fig. 3), is the same, indicating that their position as illustrated in figs. 1 and 2 is but little changed from that in life.

By far the most interesting feature of this *Medullosa* stem lies in the fusion of the steles between the A surfaces of blocks 1 and 2. It may be noted in fig. 3 that stele y has clearly united with x while the union of z with the x - y fusion is in its initial stages.

The leaf traces depart from the steles as comparatively large (slightly less than 1 mm.), nearly cylindrical masses of xylem (fig. 14a). The initial trace almost immediately starts to divide (fig. 14b), forming the numerous collateral bundles (fig. 5) scattered through the massive parenchymatous cortex between the periderm and rind. Where the bundles are still in close proximity to the steles they are usually enclosed by a distinct sheath, although this is not as strongly developed farther out in the cortex.

An especially distinctive feature of *M. Thompsonii* is the comparative paucity of fibrous tissue in association with either the bundles or the secretory canals. Conspicuous sclerenchymatous sheaths or strands such as are figured for *M. distelica* (Schopf, '39, fig. 5) and *M. Noei* (Steidtmann, '44, pl. VI, fig. 1; pl. VIII, fig. 1) are not found in *M. Thompsonii*.

Discussion of Stelar Anatomy and Comparison with Other Species.—

Stelar fusions and stelar branching were evidently frequent in the stems of the highly complex Permian species (Seward, '17, p. 104). That the same events take place in the structurally simpler species of the Anglorota group is known only in a very sketchy way. In her description of *M. centrofilis*, De Fraine noted the fusion of two steles, but at the point of fusion the steles are fragmentary (De Fraine, '14, pl. XV, fig. 2), and it was not possible to illustrate clearly the phenomenon. Scott referred to an interstelar fusion in *M. anglica* but here again the preservation was imperfect.

It is important that we have a clearer knowledge of this phase of *Medullosan* anatomy, partly in order to evaluate correctly the taxonomic use of stelar number and size, and partly to aid in interpreting phylogenetic trends in the group.

Professor Bower's investigations in the ontogeny of the ferns, the mature stelar systems of which are often rather complicated, indicate that the steles invariably started as a single protostele. It is hardly conceivable that the stelar ontogeny of the *Medullosas* could have followed any other course.

Numerous writers have compared the individual steles of *Medullosa* with the single stele of *Heterangium*. That portion of the stelar system shown in fig. 3 presents a rather close approximation to the *Heterangium* type. Whether or not the fusion of stele z with the already fused x and y steles became complete, resulting in a more nearly cylindrical (single) form, cannot be determined since the stem passes out of the coal ball shortly beyond the point illustrated. Even though the stele should assume a perfectly cylindrical form at a higher level there is, of

course, no implication that it should be referred to *Heterangium*.³ There is no doubt, however, that such a stem fragment, if found isolated, would present a striking resemblance to that genus, at least as far as the stele is concerned. Inasmuch as the seedling of *M. Thompsonii* almost certainly started with a single stele it seems likely that divisions and fusions occurred rather regularly through the length of the stem.

A number of reviews dealing with Medullosan relationships have appeared during the past few decades, and there is no cause for adding to this literature at present except for the Anglorota subgenus. This subgenus was created by Schopf in 1939 with *M. anglica* as the type species. Other species that may be included are *M. centrofilis* De Fraine, *M. pusilla* Scott, *M. distelica* Schopf, *M. anglica* var. *thiesseni* Schopf, *M. Thompsonii* Andrews, and the *Medullosa* illustrated in fig. 7 (see p. 335). There can be no doubt that these constitute a very closely related assemblage, distinct in certain seemingly valid characters, yet similar enough to justify speculation concerning their interrelationships.

Before attempting any such racial considerations it is very necessary to determine in so far as possible what characters may be of taxonomic value and what ones are too variable within an individual specimen. In order to facilitate comparison of the above seven species they are shown, all at the same magnification, on plate 12. It is evident that their structure is pronouncedly similar in spite of the considerable size difference between the large *M. anglica* and the comparatively minute *M. pusilla*. The group is a remarkable one from the viewpoint of structure and certainly a closely related taxonomic unit, and there is no longer any doubt that it was widely distributed during the Pennsylvanian. Whether the species names that have been used to designate these stems would stand if the entire plants were known is, of course, not now possible to determine. In any case, the answer would not detract from their interest, and temporarily at least they have been handled in the most expedient way.

It seems unlikely that quantitative differences, such as size of the individual steles and the number composing a stem, can be allowed to bear much taxonomic weight. In *M. anglica* alone the steles are reported to range from 6 to 30 mm. in diameter and the almost continuous range throughout the group is clearly shown in figs. 23-30. Knowing the wide variation that may exist in both primary and secondary stelar bodies of fossil and living plants (Bower, '30; Pannell, '42), such characters must obviously be regarded with considerable deliberation. Neither is the number of steles in itself an entirely dependable character. Three is apparently the "typical" number in *M. anglica*, *M. Thompsonii*, *M. anglica* var. *thiesseni*, and *M. pusilla*, and it is more than likely that fusion took place in the stem of *M. centrofilis* resulting at certain levels in three steles.

³ It should perhaps be shown that we are dealing with a fusion here and not a division; *i. e.*, that the sequence is being read in the proper direction. Although the stem fragment is short it is clear that the petiole shown in fig. 1 (from which fig. 2 is magnified) is in a more advanced state of departure some 1.5 cm. farther along the stem (from the point at which fig. 3 is taken). This is indicated by the more nearly complete development of the rind separating the petiole from the stem.

De Fraine in her discussion of the affinities of *M. centrofilis*, notes that "the agreement in practically every detail between the steles of the specimen and those of *M. anglica* and *M. pusilla*, leave no doubt as to its very close relationship with those fossils." The relative extent of endocentricity in the steles of different species may present a character of value; at least *M. distelica* seems to display this to a more marked degree than the other species. Whether or not this varies appreciably through the course of an individual stem remains to be determined when longer specimens are discovered.

Aside from these variable characters of the stelar system itself, considerable weight has been attached to the presence or absence of secondary tissues accompanying the leaf trace on its departure from the stele. This secondary wood is conspicuously abundant in *M. anglica* but was reported absent in *M. pusilla* and *M. centrofilis*, and absent or very weakly developed in *M. distelica*. It is likewise absent in *M. Thompsonii*. As far as the leaf traces themselves are concerned they appear to present a very marked uniformity in all of the species described above. The nature of the accompanying fibrous sheath may, however, be of taxonomic value.

Medullosa Thompsonii differs from *M. anglica* in the comparative rarity of secretory sacs in the cortical rind, as well as the parenchymatous middle cortex. The hypodermal cells in the two are likewise divergent in their structure (c. f. Scott, '99, fig. 13; and fig. 32 of this paper). Although the Iowa stem and *M. anglica* are undoubtedly closely related the differences that have been noted seem to justify segregation.

The differences in number, size, and extreme endocentricity of the steles, as well as abundant development of secretory sacs in the cortex, clearly set *M. distelica* apart from the Iowa specimen. Of the figures in plate 12, this leaves only *M. centrofilis* and *M. pusilla*. If size has any significance in classification the latter certainly deserves its own pigeon-hole, and the secretory canals are reported by Scott as numerous.

Although they are interesting and illustrate the size range in the Anglorota group I do not feel that either *M. anglica* var. *thiesseni* or *M. sp.* (fig. 7) is sufficiently well preserved to allow of precise comparison. *M. anglica* var. *thiesseni* and *M. Thompsonii* may very possibly be one and the same species but this cannot be verified until supplementary material of the former is forthcoming, showing well-preserved extra-stelar tissues.

Thus of the previously described species of *Medullosa* which present sufficiently well-preserved detail to allow of precise comparison, *M. centrofilis* appears to be the most closely related to the Iowa fossil. The differences are not great, the central "star-ring" and the secretory canals in the cortex of *M. centrofilis* being the only conspicuous points of divergence.

Leaves.—

Numerous isolated petioles or rachis fragments belonging to *Medullosan* stems

are present in the Urbandale coal balls. They are not only abundant but represent, as well, different branching orders of the leaves, as is clearly evinced from the size variation and the anatomy of the rind.

From a study of the literature and the material at hand, it appears that the following characters are most significant in the classification of these fossils: structure of the fibrous strands composing the rind; presence or absence of the secretory ducts, their distribution, and whether or not they are regularly associated with the fibrous strands; distribution of the vascular bundles. Use of the last character is restricted to those specimens in which there is no appreciable amount of crushing or distortion.

A number of the better-preserved specimens agree closely enough with the attached petiole bases of *M. Thompsonii* to warrant their inclusion under that species. These isolated petiole and rachis remains⁴ (figs. 9, 12, 13, 19) vary from 16 mm. (fig. 9) to a little over 4 mm. (fig. 12) in diameter. The diameter of the leaf base shown about to depart from the stem in fig. 1 measures approximately 2.2 cm. in diameter. In all probability these leaf bases tapered abruptly outward during the first few centimeters and then only very gradually to the extreme tip of the leaf, as in modern cycads and large-leaved ferns such as *Cibotium*. Figures 13 and 19 may be taken then as representing the rachis⁵ at a point some distance from the base of the leaf, and fig. 12 in turn may represent a distal secondary rachis or a tertiary one.

In the upper right portion of fig. 9 there is a localized group of a dozen or more conspicuous secretory canals scattered through, and inside of, the rind. With this exception, however, the petiole specimens referred to *M. Thompsonii* present a relative paucity of secretory canals. The lack is certainly more pronounced than in previously described species and compares closely with the similar negative feature of the leaf bases in organic connection with the stem.

One of our coal ball specimens contains a number of leaves of the *Alethopteris* type, most of which have been cut in transverse sections. Although there is considerable reason to believe that certain species of this genus were borne by the *Medullosas* it must be admitted that the present report does not further our knowledge of that relationship. However, certain features of these Iowa specimens do contribute toward a clearer understanding of their structure.

The restoration shown in pl. 13 is a composite drawing compiled from the best-preserved portions of a dozen or more leaflets. The coal ball containing the pinnules is highly pyritized, although that mineral has not penetrated the leaf tissues to any appreciable extent. Both peel preparations and ground sections proved unsatisfactory for photographic reproduction.

⁴ It may be noted that the illustrations of these petiole and rachis fragments in transverse section are all reproduced at the same magnification. Although it necessitates considerable variation in figure size I believe that if this practice could be more generally adhered to it would greatly facilitate the distinction between different species as contrasted with the differences represented by the ordinal position of the leaf part represented.

⁵ In view of the rather irregular dichotomy of the frond of *Alethopteris* and certain related species (Bertrand, '32) the term rachis is used here rather loosely to signify the larger proximal branches of the petiole.

Within the epidermis there is a clearly defined hypodermal layer and under this a third seriation of cells differing from the hypodermal in their vertical alignment. In all probability they were chlorophyllous in life, functioning as palisade cells.

The under-side of the leaflets presents a conspicuous combination of short papillose cells and long multicellular hairs. The cells densely cover almost the entire under-side, and in all probability the stomata were located among their swollen bases. It has not been possible to identify the guard cells. The elongate multicellular hairs are most striking (fig. 11). Most of them have been broken, but the few apparently entire ones consist of five or six cells. Within the epidermal papillae there is a zone of compact, more or less isodiametric, angular cells. The tissue between this and the palisade cells is very poorly preserved. However, I have observed that the region in close proximity to the central vein is occupied by loosely organized, horizontally arranged cells. There is no reason to believe that these did not extend to the margin of the leaflet as shown, although it should be noted that this feature of the restoration is uncertain. Nor has it been possible to distinguish with clarity the structure of the vascular tissue.

Sections of presumably Alethopterid leaves found associated with Medullosan petioles have been described and figured by Scott, '99, Steidtmann, '44, and Schopf, '39. Scott (p. 101) notes: "I have not yet found absolute proof that these leaflets belong to the '*Myeloxylon*' rachis, but the constancy of association, and general agreement in the structure leaves no real doubt." This opinion seems to be shared by Schopf and Steidtmann in their respective treatments of *M. distelica* and *M. Noei*.

The general similarity among the leaves illustrated by Scott and Steidtmann and our Iowa specimens lends support to this relationship with the *Myeloxylon* petiole remains. The distinctive multicellular hairs are illustrated in Steidtmann's specimens although these are not indicated in the English material. Nor is the hypodermal layer of cells indicated in Scott's fig. 17, although the preservation of his material apparently was rather inferior in this respect.

There is also a striking resemblance between the anatomy of the fossil leaflets and those of the living cycads (fig. 10). Assuming that the elongate spongy mesophyll cells are uniform through the width of the fossils the two are very nearly identical, with the exception of the multicellular hairs that are lacking in *Cycas revoluta*.

Roots.—

A number of isolated roots have been found in the Urbandale petrifications. Many of them compare closely enough with those described by Steidtmann ('44) and Schopf ('39) as to leave no doubt of their Medullosan affinities. It is not possible, however, to refer them with certainty to any species of the genus.

Most of the roots are tetrarch (fig. 15) and show various stages in the development of the secondary xylem. One is hexarch (fig. 16) although the stele is enclosed by a band of periderm characteristic of Medullosan roots.

The Restoration (pl. 13)—

The conspicuous role that the *Medullosas* evidently played in Pennsylvanian landscapes makes some sort of restoration of these plants desirable. Although the plant shown in pl. 13 is captioned "a *Medullosa* of the Anglorota group" it is based primarily on the stem and leaf remains of *M. Thompsonii*. However, aside from differences in size, there is no reason to believe that the Anglorota species presented any great dissimilarity in their general habit. In order that this restoration may bear no false implications or in any way convey impressions that do not rest on established facts the following points should be clearly understood: We do not know the exact height of any species of this group, but judging from the relatively small amount of supporting tissue they were probably not more than a few feet high,—perhaps 3–5 feet is self-supporting. If the plants attained greater heights let us assume up to 15 or 20 feet, it is likely that they grew in rather dense stands and supported one another, or relied upon the trees and shrubs of other species.

The fronds were large in proportion to the diameter of the stems, and in order to arrive at a reasonable approximation of their size, measurements have been made of ten living species of cycads as well as a species of *Cibotium* growing in the Garden greenhouses. In the cycads there is a rather constant ratio between the basal diameter of the petiole and the length of the leaf. However, Alethopterid leaves possessed a considerably higher breadth/length ratio than modern cycads, probably lying closer to that of a *Cibotium* frond. Yet from the structural similarity of the *Alethopteris* leaflets and those of a modern cycad it is certain that the weight of a *Medullosa* leaf, for its total area, was much closer to the cycads than a large-leaved fern. These points have been duly considered in determining the size of a *Medullosa* frond, relative to stem diameter, based on petiole diameter measurements.

As for the morphology of the leaves, indications are that the primary rachis gave rise to successive unequal bifurcations in at least some species of *Alethopteris* and related form-genera (Bertrand, '32, p. 67; Kidston, '11, fig. 7). It is reasonable to assume that the leaf size varied appreciably in the different species of the Anglorota group. Although the stem as shown in the restoration probably bore a crown of perhaps six to a dozen (more or less) leaves more precise detail could be shown if only one leaf were drawn in. Furthermore, the leaves were probably borne in a manner comparable with that of modern tree-ferns although the single leaf shown has been illustrated so as to conserve space and at the same time bring out the salient features of its construction.

Reproductive structures have been omitted from the drawing. Although seeds have been found on *Alethopteris* leaves (Halle, '29) and they are abundantly associated with the stems in the Iowa coal balls, it seemed best to postpone this feature of the restoration until further evidence is forthcoming.

Diagnosis of Medullosa Thompsonii Andrews.—

Stem approximately 3.6 cm. in diameter, epidermal cells radially elongated,

fibrous cortical strands circular to slightly elongated radially and anastomosing only at extended intervals, secretory canals rare in outer cortical (rind) region, internal periderm present; stelar system of three endocentric steles fusing upward, leaf trace sheaths poorly developed.

Petioles approximately 2.2 cm. in diameter at point of departure from stem, secretory canals not abundant.

Locality: Urbandale Coal Mine, Des Moines, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type specimen: No. WCB420, Henry Shaw School of Botany, paleobotanical collections.

Other Medullosan Stems.—

Fragments of other stems, recognizable as belonging to the genus *Medullosa*, are included in our collection from the Urbandale mine. Although not sufficiently well preserved to merit specific recognition, one is worth a brief note. As shown in fig. 7 only the steles, of which there are two, are preserved. The periderm is sufficiently intact to indicate that no more than two were originally present. Aside from this, all extra-stelar tissues have been destroyed. The smaller stele measures 8.0 x 4.0 mm., and the larger 15.5 x 4.0 mm. although it is obviously crushed, probably nearer 15.5 x 6 mm. in life. Both are slightly endocentric, but this feature is much more pronounced in *M. distelica*, the only other known bistelar species. It is also appreciably smaller than *M. distelica* (see pl. 8), being more or less intermediate in size between that species and *M. Thompsonii*.

Myeloxylon Bendixenii sp. nov.

Included in the Medullosan petiole specimens from the Urbandale mine is one that is decidedly different from those described above as *Medullosa Thompsonii*. This petiole is large, as compared with the others, measuring approximately 3 cm. in diameter although it was somewhat compressed prior to fossilization (fig. 8). Since the most distinctive features lie in the structure of the rind a representative portion of this is shown in detail in fig. 35. Within the epidermis there is a band of parenchymatous cortex, 5–6 cells deep. This in turn encloses a broad and very conspicuous fibrous zone which averages nearly 2.0 mm. thick. The radial and tangential dimensions of the fiber bundles are more or less equal although many of them are quite irregular. A glance at fig. 8 reveals more in this respect than could be conveyed by many pages of measurements.

With the exception of the outermost strands almost every strand is associated with a secretory duct on its outer side (fig. 35). These ducts average 190 μ in diameter.

As may be noted in fig. 8, there are a few fibrous strands scattered deep within the petiole. The secretory ducts, with their conspicuous black contents, are also numerous in the ground parenchyma scattered among the vascular bundles. The large size of this petiole, as well as the anatomical details of the rind, leaves little doubt that it is not to be associated with *Medullosa Thompsonii*. Thus, until more

stem remains are retrieved from Iowan petrifications it must be referred to *Myeloxylon*.

A comparison with other American species reveals no close alliance with previously described specimens. Penhallow's *Myelopteris* (*Myeloxylon*) *topekensis* (Penhallow, '97) is not sufficiently well preserved to allow comparison. Arnold and Steidtmann ('37) proffered the same opinion concerning this species, and there seems to be no justification for further reference to it in the literature, since its exact origin is also not known.

Myeloxylon Bendixenii differs from both *M. missouriensis* Arnold & Steidtmann ('37), and *M. zonatum* Steidtmann ('44) in the following respects: the rind of *M. Bendixenii* is twice as thick; secretory canals are much more abundantly associated with the fibrous strands; and the inner border of the rind is not as sharply delimited.

Diagnosis of Myeloxylon Bendixenii Andrews.—

Petiole large (3 cm. diam.), parenchymatous cortex 5–6 cells deep between epidermis and rind, rind (fibrous zone) 2 mm. thick radially, fiber bundles more or less isodiametric in transverse section, almost every bundle accompanied by a secretory duct on outer side, ducts averaging 190 μ in diameter.

Locality: Urbandale Coal Mine, Des Moines, Iowa. (see p. 323.)

Horizon: Pennsylvanian, Des Moines Series.

Type specimen: No. WCB429, Henry Shaw School of Botany, paleobotanical collections.

This species is named in honor of Charles Shuler Bendixen, an official of the Shuler Coal Mine, located eight miles west of Des Moines, Iowa.

Schopfiastrum decussatum, gen. et sp. nov.

The following description is based on two stem fragments also found in coal balls from the Urbandale mine near Des Moines. Although much remains to be learned of the plant as a whole the available information indicates a pteridosperm with strikingly distinct anatomical features, particularly the structure and arrangement of the leaf traces. It is intended that this paper serve only as a preliminary report to be supplemented by a full account when more complete specimens are forthcoming. Of the two specimens at hand, one (WCB434) consists of a decorticated stele, and another (WCB421) in which both stele and outer cortex are preserved.

Judging from the more complete specimen (fig. 17) the stem was about 21 mm. in diameter. The specimen illustrated (measuring 9. x 30. mm.) appears collapsed due to decay of the internal cortical tissues. However, there is no reason to believe that the stem was not cylindrical or nearly so in life.

The primary wood is rather sharply 4-angled in transverse section, measuring 2. mm. on a side, and is composed of elongate tracheids with some interspersed parenchyma. The infiltrations of pyrite, as well as occasional cracks (fig. 18), have destroyed a few of the cells. The parenchyma cells were relatively few, far

less than in pteridosperm stems (presumably the most closely related to this genus) such as *Rbetinangium* and *Heterangium*.

In both their structure and order of departure from the stele the leaf traces differ in striking fashion from any other stem that has been referred to the Pteridospermeae. In the stem shown in fig. 17 it may be noted that, although the primary xylary tissues are crushed, the two leaf traces appear to be diametrically disposed, that is, 2-ranked. This opposite arrangement is confirmed in the other specimen (WCB434) in which the primary wood is somewhat better preserved (fig. 18).

At the earliest observed point in its departure from the stele the trace is already bilobed (fig. 18, lt₂) and its cross-sectional size is equal to fully half that of the cauline primary xylem. Even at this level, however, each lobe has in turn started to divide, there being four exarch protoxylem groups in the trace. Reason for believing that these four originated from two exarch groups in the primary stele will be given below. In following this leaf trace through the length of the specimen (3 cm.) very little change takes place, but the opposite trace, as well as the one shown in fig. 17 (from specimen 421), reveals at least some of the subsequent changes. The trace as a whole becomes strongly 4-lobed and tangentially elongate with the protoxylems occupying the outermost tip of each lobe. Shortly prior to its departure from the stele the protoxylem groups in the distal lobes of the trace divide (fig. 18, pxt). It is not known whether further lobing or actual division occurs in the traces at a higher level.

Judging from the difference in the structure of a pair of traces at any one point, it is evident that one departed appreciably in advance of the other. The origin of the succeeding pair of traces may next occupy our attention. In two of the ground sections prepared from specimen 434, four exarch protoxylem groups are clearly defined in the stele. These are paired, and alternate with the leaf traces, as shown in fig. 18, pxs. It seems most probable that the next pair of traces will have their origin from these protoxylem points, although confirmation of this must await the discovery of longer stem fragments.

Judging from these opposite pairs of protoxylem groups, an individual trace started with but 2. Shortly following segregation of the trace from the primary stele of the stem each protoxylem divided, resulting in 4, and this was then followed by the lobing of the traces as a whole into 4 parts.

As the traces increased in their tangential dimensions in passing through the secondary wood they left a broad gap in that tissue and a small quantity of secondary wood accompanied the trace on its outer face (fig. 22, x 2).

The secondary xylem of the stem is strongly developed, attaining a maximum radius of nearly 3 mm. The shape of the tracheids as seen in transverse section is of the irregular angular type found in other pteridosperm stems (Andrews, '40, p. 89) such as *Lyginopteris* and *Medullosa* (Anglorota section), and their radial walls are covered with closely compacted angular bordered pits. The same type of pitting is also found in the metaxylem tracheids.

The outer cortex is constructed of thin longitudinal-radial plates of fibers

(fig. 20) rather regularly spaced with parenchymatous cells. Although the latter vary appreciably in size most of them are characteristically elongated (140. x 80. μ) in a tangential direction. The fibrous strands anastomose only at extended intervals, appearing in tangential section (fig. 21) as nearly parallel strands. This fibrous zone of the cortex is separated from the epidermis, the cells of which measure 35. x 20. μ , by a single row of cortical parenchyma cells considerably smaller than those deeper within.

Diagnostic Summary of the Genus Schopfiastrum.—

Outer cortex composed of nearly parallel radial-longitudinal fibrous strands separated by tangentially elongated parenchyma cells; secretory canals absent or very rare; primary xylem a mixed protostele, protoxylem exarch, two opposite pairs present in internodes; leaf traces large, soon becoming bilobed and accompanied at least to the inner cortex by a small amount of secondary wood; traces arranged in opposite pairs, one of each pair departing ahead of the other, the succeeding pair of traces alternating; secondary wood present, with closely compacted, reticulate-bordered pits on radial walls of tracheids.

Locality: Urbandale Coal Mine, Des Moines, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type specimens: Nos. WCB421 and WCB434, Henry Shaw School of Botany, paleobotanical collections.

The genus is named for Dr. James M. Schopf, of the United States Bureau of Mines, in recognition of his contributions to Carboniferous paleobotany.

Discussion.—

The genus *Schopfiastrum* is considered referable to the Pteridospermeae in view of the characteristic fibrous outer cortex, the structure of the leaf traces which compares in a general way with that of *Rbetinangium* and *Heterangium*, and the closely compacted reticulate pitting of the tracheids as well as their shape as observed in transverse section.

The closest affinities of *Schopfiastrum* seem to lie with the genera *Rbetinangium* and *Heterangium*. In fact, during the earlier phases of this investigation the stem was tentatively considered as a new species of *Rbetinangium*. However, when the structure of the primary xylem and the organization of the traces had been worked out this treatment was found to be quite untenable. The outer cortex is very similar to that of *Rbetinangium arberi* Gordon ('12), both possessing the distinctive tangentially elongated parenchyma cells between the fibrous strands. However, *Schopfiastrum* lacks the secretory canals, with their radially arranged epithelial parenchyma, which are present in the outer cortex of *Rbetinangium*. A few apparent canals have been observed in this region but in almost all cases they are clearly the result of fungous or bacterial action. The leaf traces of the Iowa stem are comparable with those of *R. arberi*, in their massive size and exarch protoxylems but the comparison goes no further. In *Rbetinangium* the trace is composed of a number of irregularly U-shaped strands interspersed with

parenchyma, quite different from the predominantly tracheidal unit traces of *Schopfiastrum*.

There is no evidence in the Iowa stem of horizontal sclerotic plates in the inner cortex such as are found in *Heterangium*. The single leaf trace (to each petiole) of *Schopfiastrum* precludes any close relationship with the polydesmic Heterangiums and differs markedly in size, form, and arrangement from any of the Eu-heterangium species.

Schopfiastrum is of special interest not only in its clearly defined generic characters, but, judging from the structure of the primary wood, it is a rather primitive pteridosperm. As stated above, it seems to lie as close to *R. arberi* as any described pteridosperm yet the protostele of *Schopfiastrum*, its less complex leaf traces, and the lack of secretory canals in the cortex, all point toward a less specialized plant. Also, the monotypic *Rbetinangium* was found in the middle Lower Carboniferous of Scotland while *Schopfiastrum* is of much more recent origin, coming from middle Upper Carboniferous rocks. This is an apparent paradox that is by no means unique in paleobotany and at least offers assurance that there are many more unknown species and genera in the Seed-fern group that remain to be found.

Appendix I.

The late Professor A. C. Noé is quite justly acknowledged as having been the first person to collect coal balls in this country, nearly 25 years ago, and to him is due most of the credit for initiating interest in their study. However, Mr. F. O. Thompson has recently brought to my attention a point of historical interest pertaining to an earlier discovery of coal balls in America that seems worth mentioning.

In Volume II of the Iowa Geological Survey Reports Dr. C. R. Keyes ('94) reported the presence of coal balls (although they were not described under that name) in the Bloomfield mine near Des Moines. To quote directly from this account:

Associated with the coal bed are numerous lenticular masses of ironstone. They vary in size from a few inches to ten or twelve feet horizontally, and up to six feet vertically. The smaller ones are commonly called "nigger heads." These segregations occur in all parts of the coal seams, but they are most abundant in the roof and upper surface of the coal, where they are often so close together as to form an almost continuous layer. It is common for the nodules in the upper part of the coal to project upwards above the top of the seam, often two to three feet in case of the large masses. They are covered usually by a few inches of carbonaceous material. [pp. 279-281].

In the Annual Report for 1896 A. F. Bain ('97) reported the presence of "clay-ironstones" in the Bloomfield mine and several others, and he notes that: "An analysis of similar material from a mine in Mahaska County showed the presence of about 88 per cent of limestone, with 8 per cent of organic matter and small percentages of iron oxides and sulphides." (p. 297)

The authors in both instances figure vertical sections through the coal showing the coal balls ("ironstones") in the upper portion of the seams. Thus there is no

possibility of their being confused with the sterile slate-gray concretions common in the overlying shales, and also referred to by the miners as "nigger heads." The presence of 8 per cent organic matter removes any doubt as to their identity, and the high percentage of limestone reported by Bain also suggests coal balls of fine quality. At least his figures leave little room for the obnoxious iron sulphide.

These petrifications, although apparently well known to geologists, did not reach the hands of paleobotanists until a quarter of a century later when Noé started collecting in Illinois.

Appendix 2.

Medullosa anglica var. *thiesseni* was described by Schopf in 1939 although at that time its origin was unknown beyond the knowledge that it had been collected in the "western coal fields of this country." The horizon from which var. *thiesseni* came has now been established and the information is presented here, with Dr. Schopf's permission, in order that the record of the western *Medullosas* may be as complete as possible.

The specimens upon which Schopf's ('39) description were based were found by R. V. Pepperberg in southeastern Nebraska in 1907. Three years later Pepperberg described a Carboniferous flora, in which *Neuropteris* predominated, from two localities, one near Nebraska City (Otoe Co.) and the other near Peru (Nemaha Co.). It is not clear at which locality the specimens were found but the horizon is believed to be the same. The specimens are mentioned on p. 330 (Pepperberg, '10) in a letter addressed to him by David White. The generic identity of the specimens was established by Reinhardt Thiessen, for whom they were later named.

In 1936 Pepperberg's collections were referred to by Elias ('36) as follows:

19. Near the top of the Table Creek shale formation. The well-preserved flora, collected in soft sandy shale 1½ feet below the Dover limestone, contains *Neuropteris* and *Annularia*. Probably from this horizon came the flora consisting of numerous *Neuropteris* leaves and *Calamites* stems in sandstone and sandy shales at Brownville, Nemaha County, Nebraska . . . and at Nebraska City, Otoe County, Nebraska (7, p. 313).⁶

In 1943 Condra and Reed reported that "the so-called 'Table Creek shale' represents three formations, i. e., the shale below the Dover (with the Maple Hill limestone missing), plus the sandstone equivalent of the Tarkio, plus the Willard shale." In the stratigraphic column given by Condra and Reed (p. 42) the "Table Creek" is from the lower part of the Richardson sub-group. The latter is the upper sub-group of the Wabaunsee group which is the uppermost part of the Virgil series.

It is of considerable interest to find a *Medullosa* of the Anglorota group from such a high horizon. All of the English species were derived from the Lower Coal Measures, well down in the lower part of the Pennsylvanian. The American *M. distelica* and *M. Thompsonii* likewise are from horizons considerably below the Table Creek shale. Thus it is evident that the *Medullosas* of the *anglica* type were not only widely distributed geographically but that this racial life span extended over many millions of years.

⁶ This is a reference to Pepperberg's 1910 paper.

Acknowledgment.—

The addition of this chapter to American coal ball studies has been made possible through a gift from Mr. Frederick O. Thompson of selected specimens from his own collections. For his generous support and continued interest in the scientific progress of the investigation we are profoundly grateful. Thanks are also due Mr. R. M. Kosanke for the loan of slides of *Medullosa anglica* var. *thiesseni* from the collections of the Illinois Geological Survey; and to Mr. F. Tracy Hubbard for the loan of Iowa coal ball slides from the Botanical Museum of Harvard University. I am indebted to Dr. James M. Schopf, The United States Bureau of Mines, for many helpful suggestions pertaining to the taxonomy of *Medullosa*.

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EXPLANATION OF PLATE

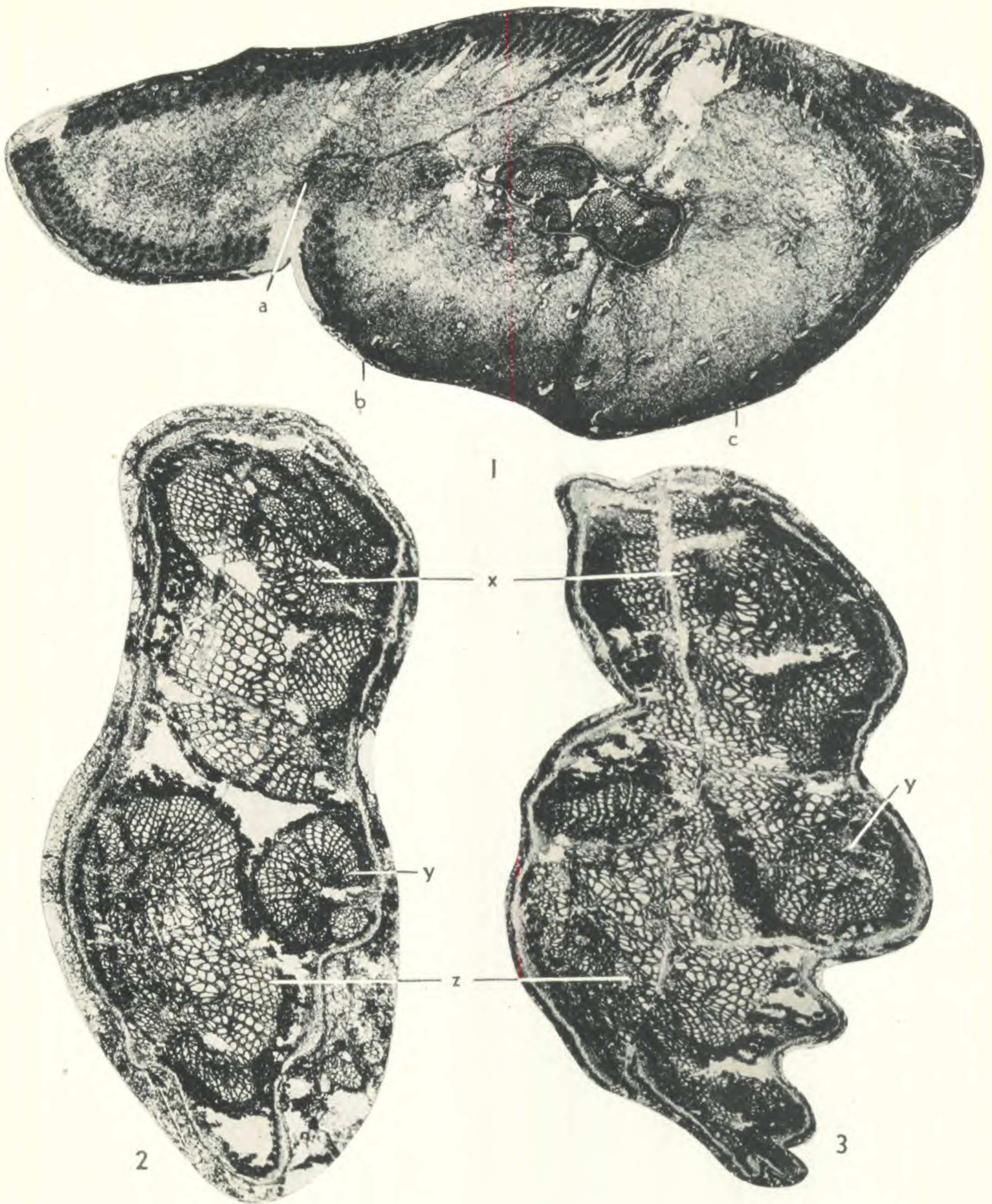
PLATE 5

Medullosa Thompsonii Andrews

Fig. 1. The stem in transverse section showing a leaf trace departing at the left. *a*, fibrous strands separating stem from leaf base; *b*, *c*, between these two points the cortical rind is lacking, explanation in text. WCB420-2-A3, x 2.3.

Fig. 2. Stellar system from fig. 1 shown at a higher magnification. *x*, *y*, *z*, steles. WCB420-2-A3, x 7.0.

Fig. 3. Showing fusion of the three steles. WCB420-1-A3, x 7.0.



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII

EXPLANATION OF PLATE

PLATE 6

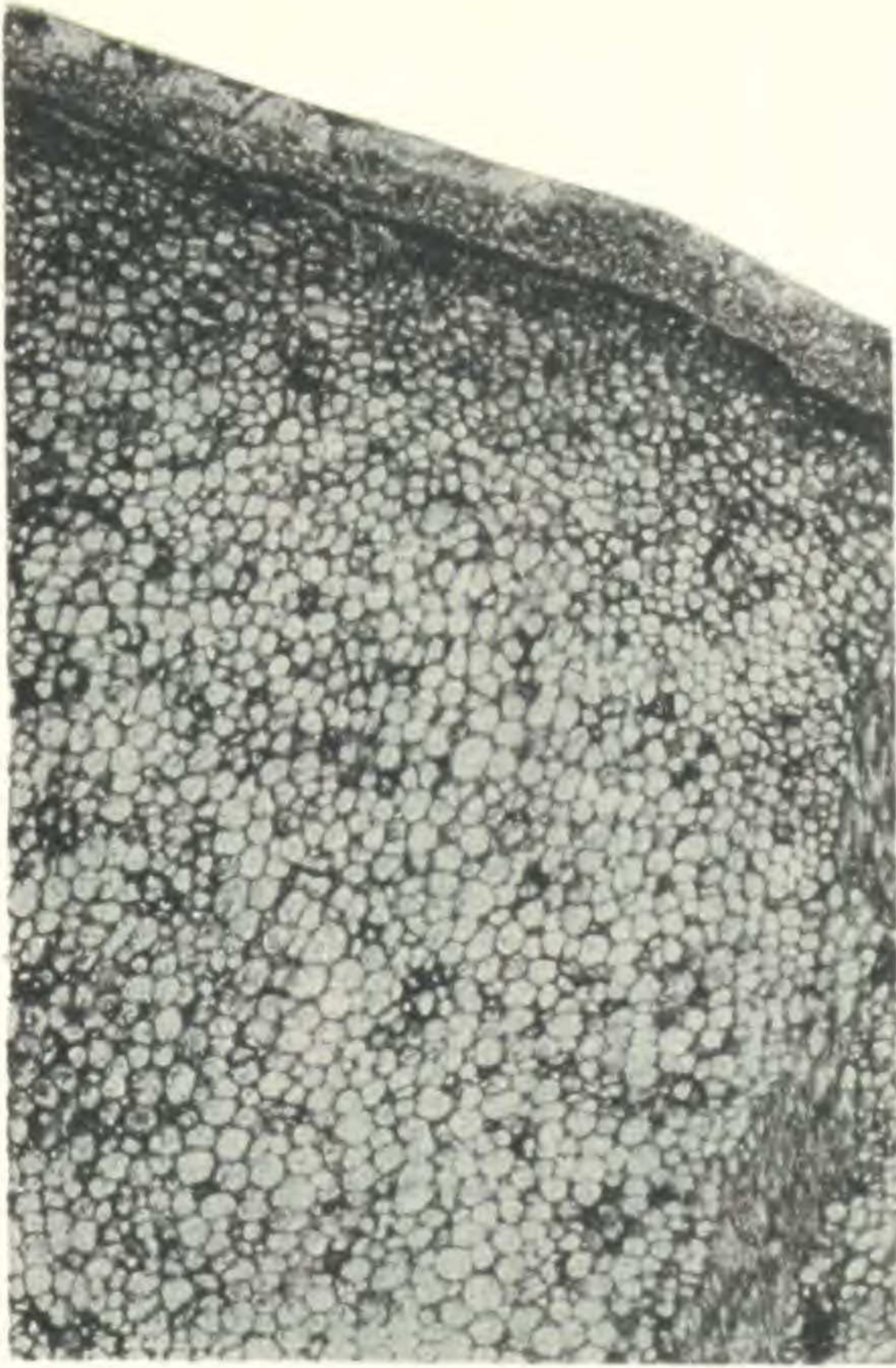
Medullosa Thompsonii Andrews

Fig. 4. Transverse section through outer cortex as that tissue appears between points *b* and *c* of fig. 1. Slide No. 1363, x 17.5.

Fig. 5. The rind or outer cortical fibrous tissue of the stem. Slide No. 1364, x 17.5.

Fig. 6. A single vascular bundle from the petiole shown in fig. 9. WCB426, Slide No. 1368, x 76.

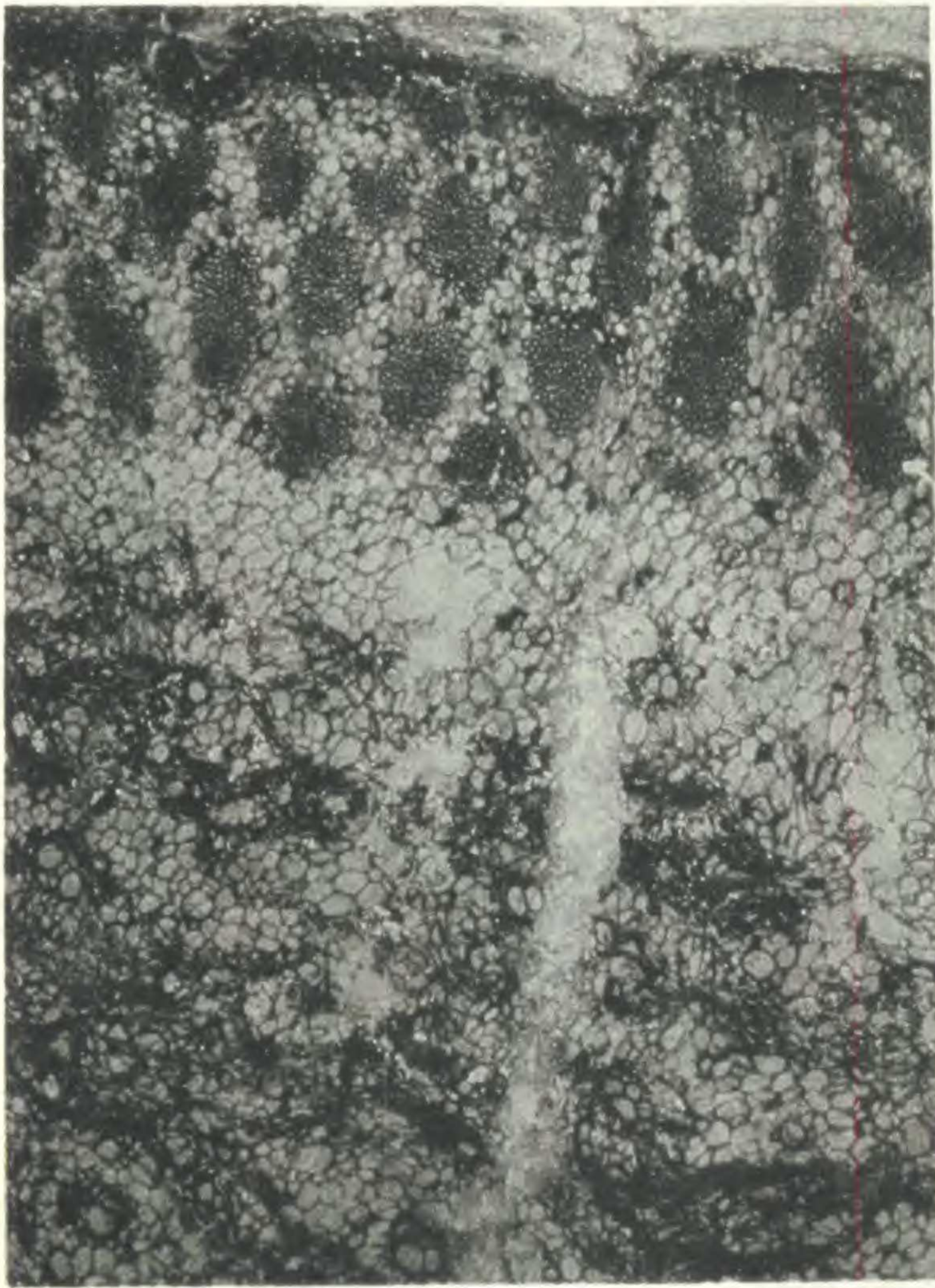
Fig. 7. *Medullosa* sp. A bistelar Medullosan stem. Explanation in text. WCB461, x 4.2.



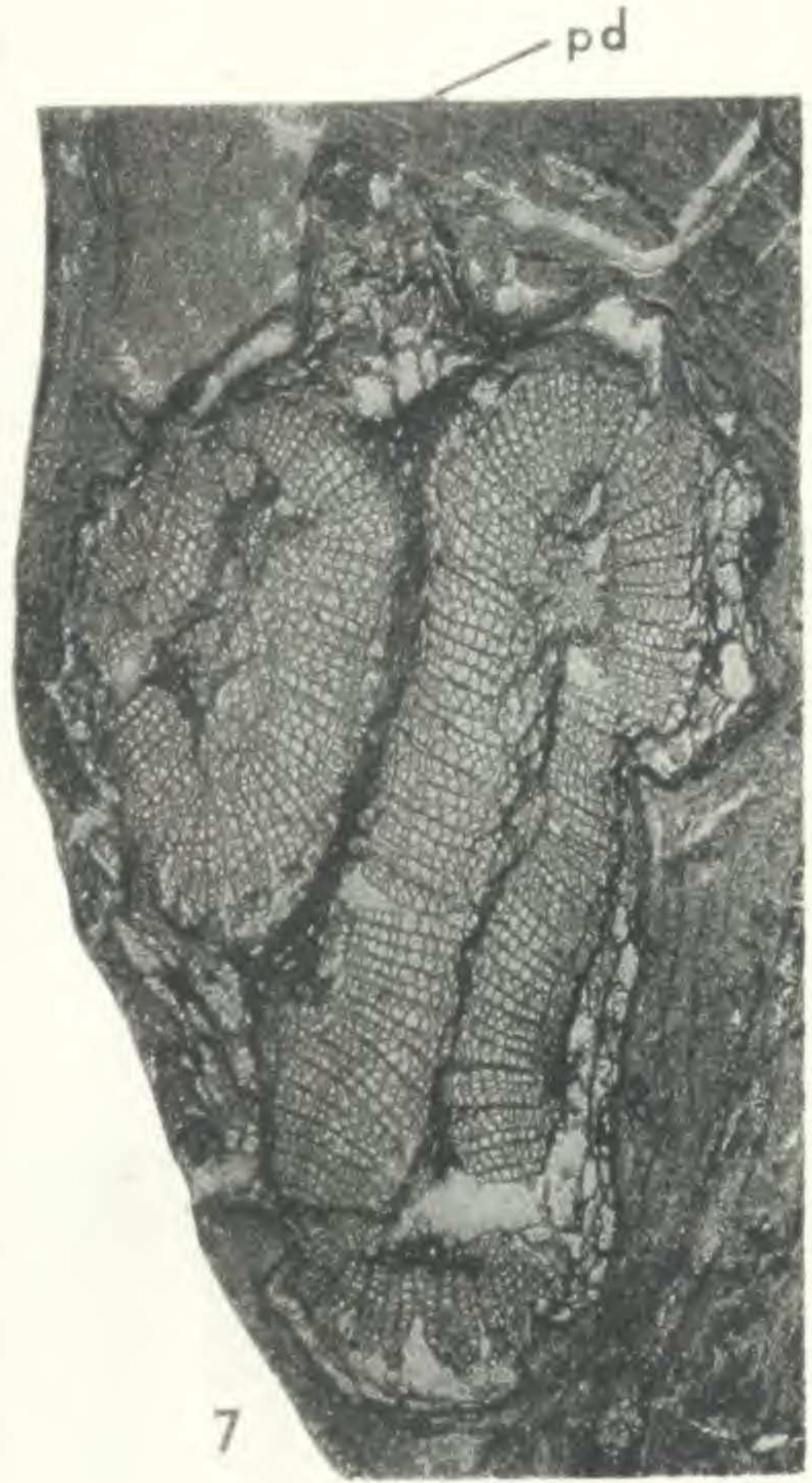
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6



5



7

EXPLANATION OF PLATE

PLATE 7

Myeloxylon Bendixenii Andrews

Fig. 8. Transverse section showing the greater part of the petiole. WCB429-S2,
x 10.2.



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII

EXPLANATION OF PLATE

PLATE 8

Medullosa Thompsonii Andrews

Fig. 9. An isolated petiole believed to be referable to the stem species shown in fig. 1.
WCB426-T2, x 10.2.



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII

EXPLANATION OF PLATE

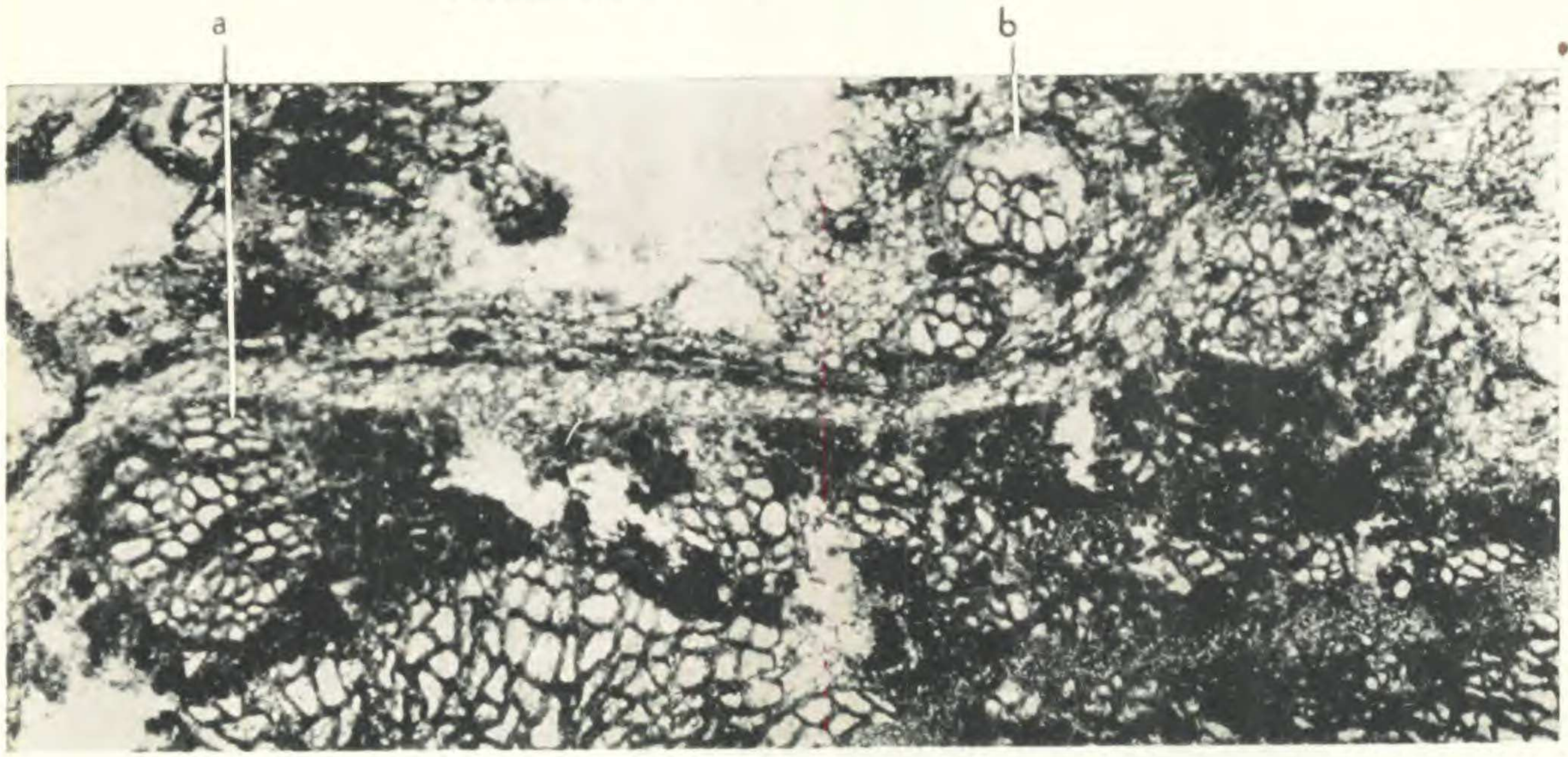
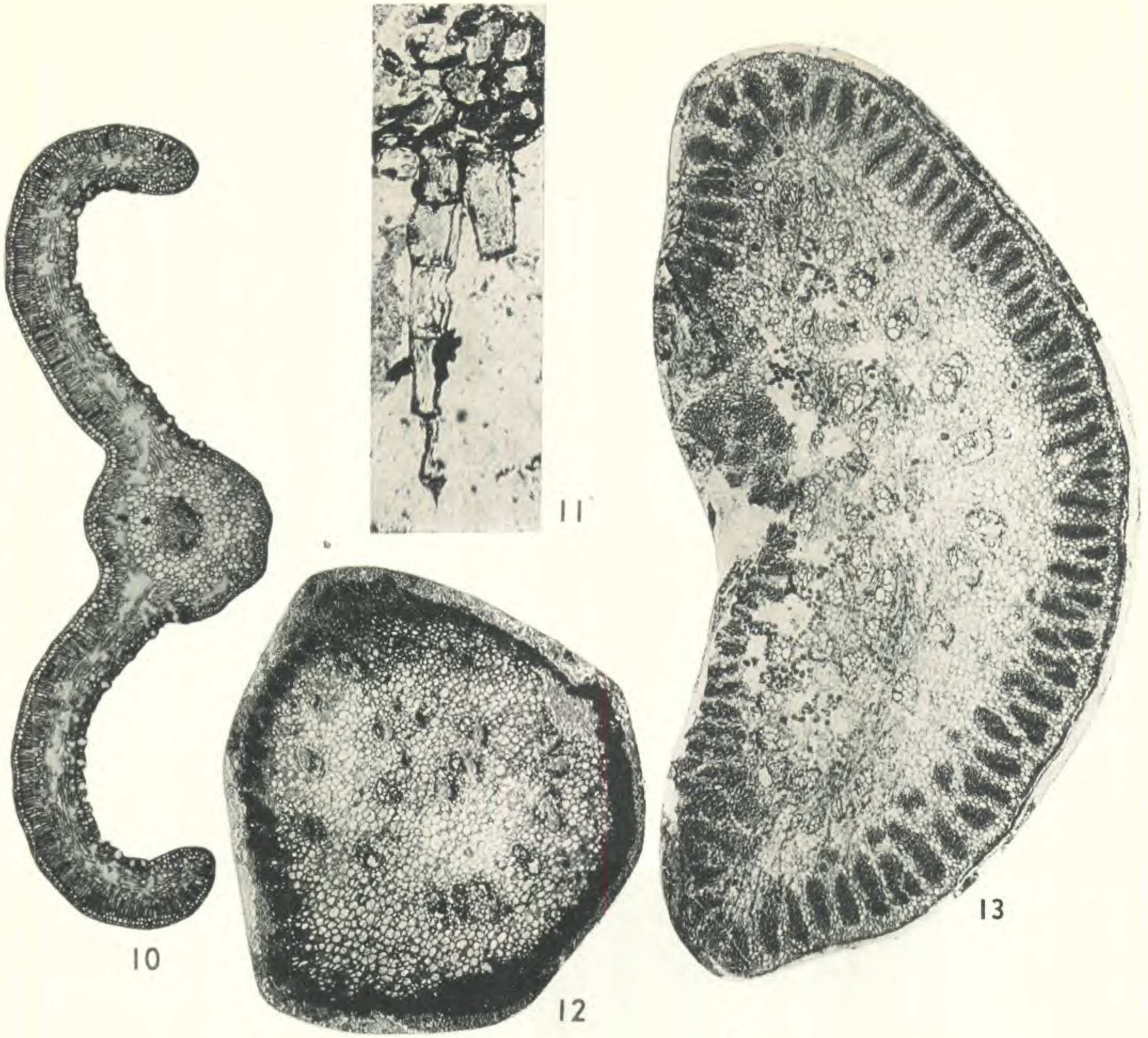
PLATE 9

Fig. 10. Transverse section of a leaflet of the living *Cycas revoluta*, x 20.2.

Fig. 11. Showing a large multicellular hair, and basal portion of another, from the lower epidermis of an *Alethopteris*-like leaflet. Slide No. 1369, x 99.

Figs. 12, 13. Transverse sections of rachis branches believed to be referable to *Medullosa Thompsonii*: fig. 12, WCB433-T1, x 11; fig. 13, WCB429-S2, x 10.2.

Fig. 14. A portion of the outer stelar region of *Medullosa Thompsonii*, showing departing leaf traces. WCB420-2-B3, x 22: *a*, leaf trace shortly after departure from stele; *b*, leaf trace dividing.



14

EXPLANATION OF PLATE

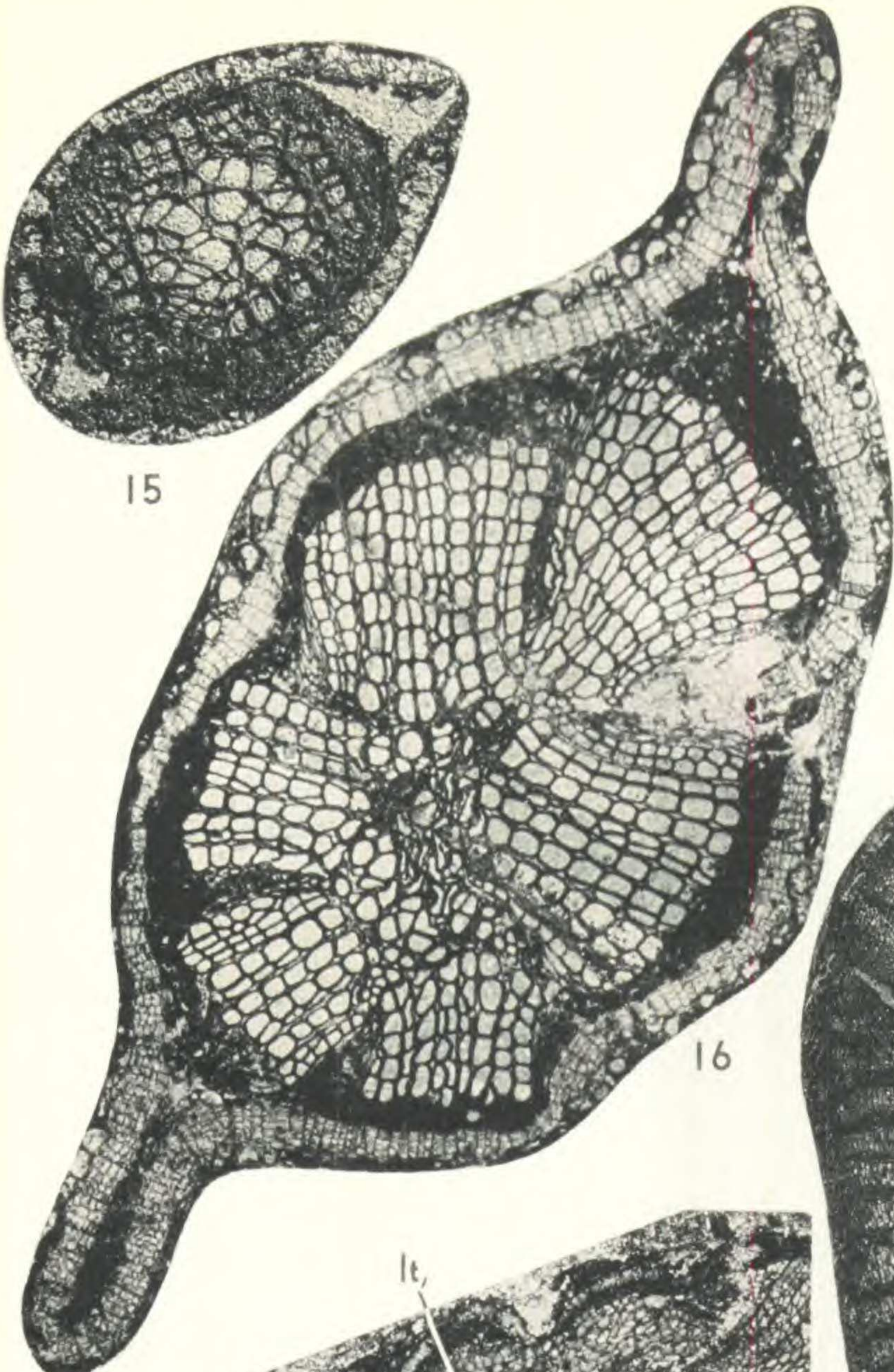
PLATE 10

Figs. 15, 16. Roots found in coal balls associated with the Medullosan stems: fig. 15. WCB462, x 14; fig. 16. WCB422, x 14.

Schopfiastrum decussatum Andrews

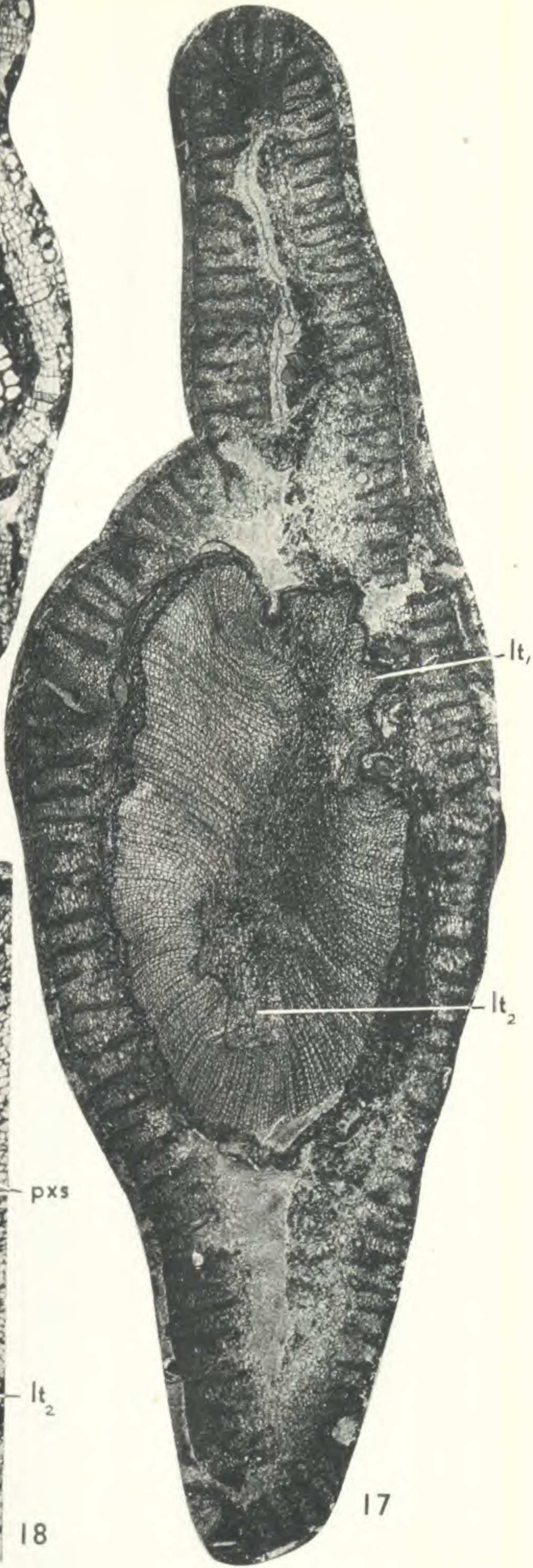
Fig. 17. Entire stem in transverse section: lt_1 and lt_2 , leaf traces. WCB421, x 6.5.

Fig. 18. Showing central portion of stem (from another specimen) at a higher magnification: lt_1 , lt_2 , leaf traces; pxs, protoxylem groups of stele; pxt, protoxylem groups of trace. WCB434. Slide No. 1353, x 11.



15

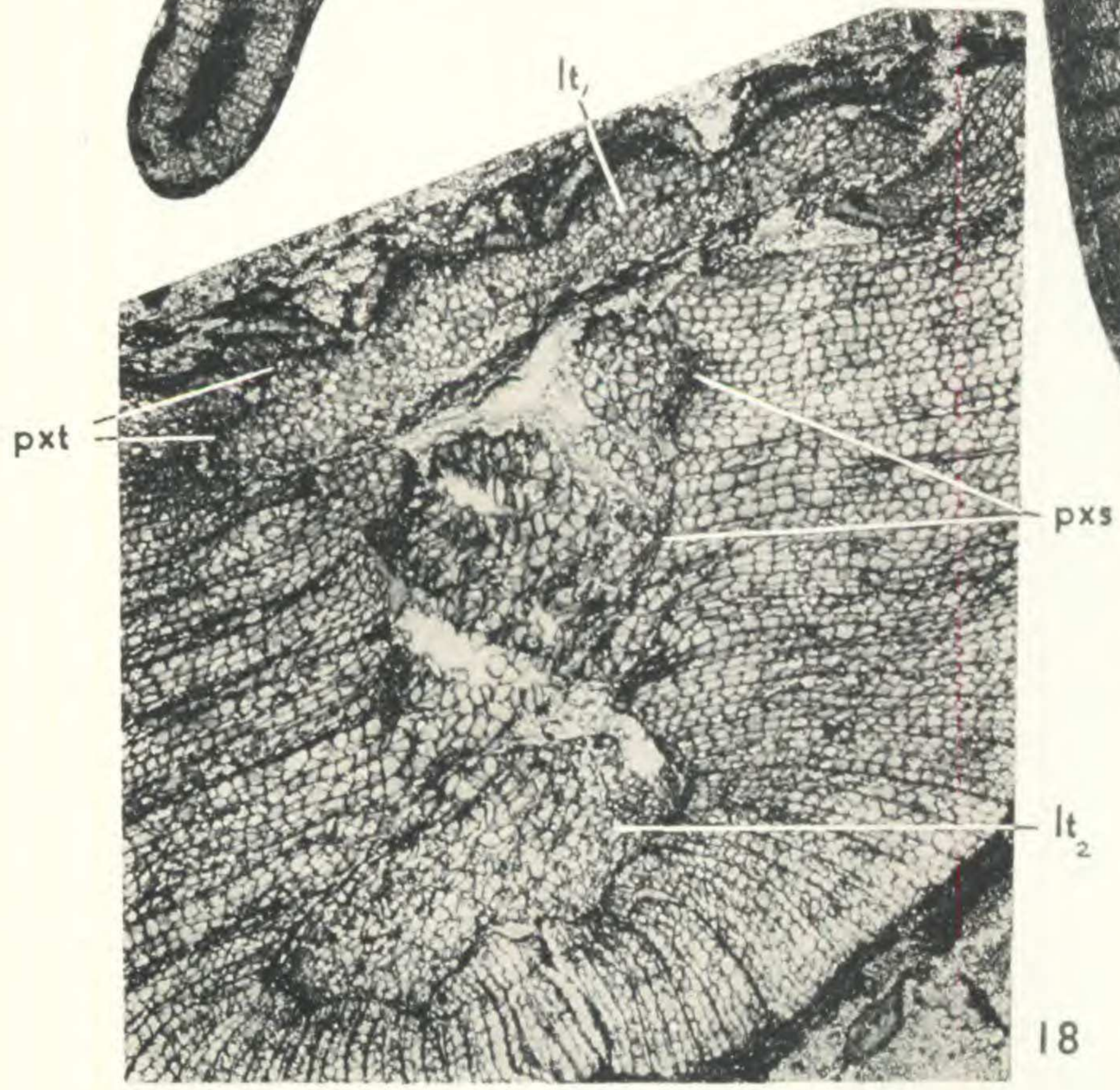
16



lt_1

lt_2

17



pxt

pxs

lt_2

18

ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII

EXPLANATION OF PLATE

PLATE 11

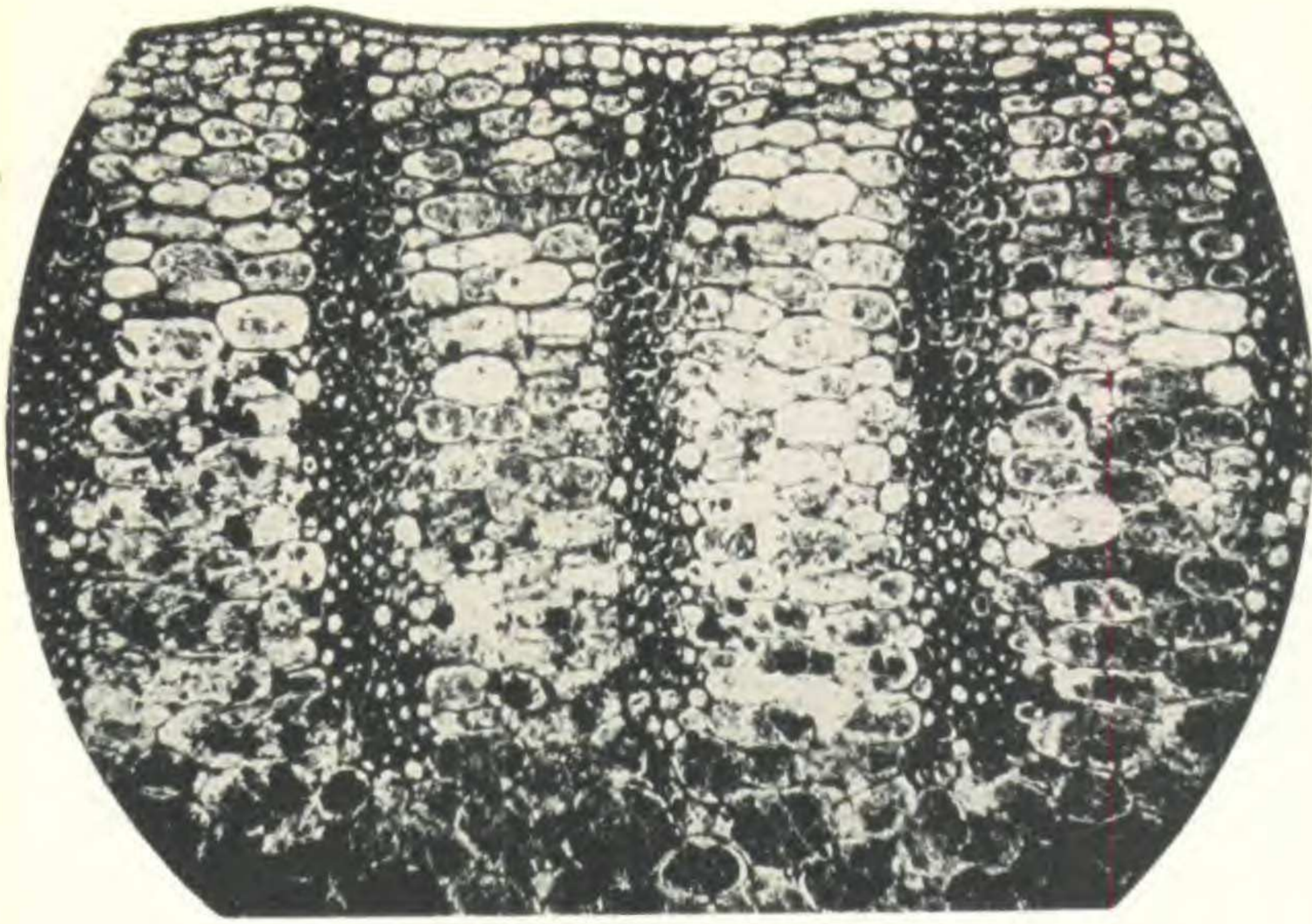
Fig. 19. Transverse of rachis branch believed to be referable to *Medullosa Thompsonii*. WCB427, x 10.2.

Schopfiastrum decussatum Andrews

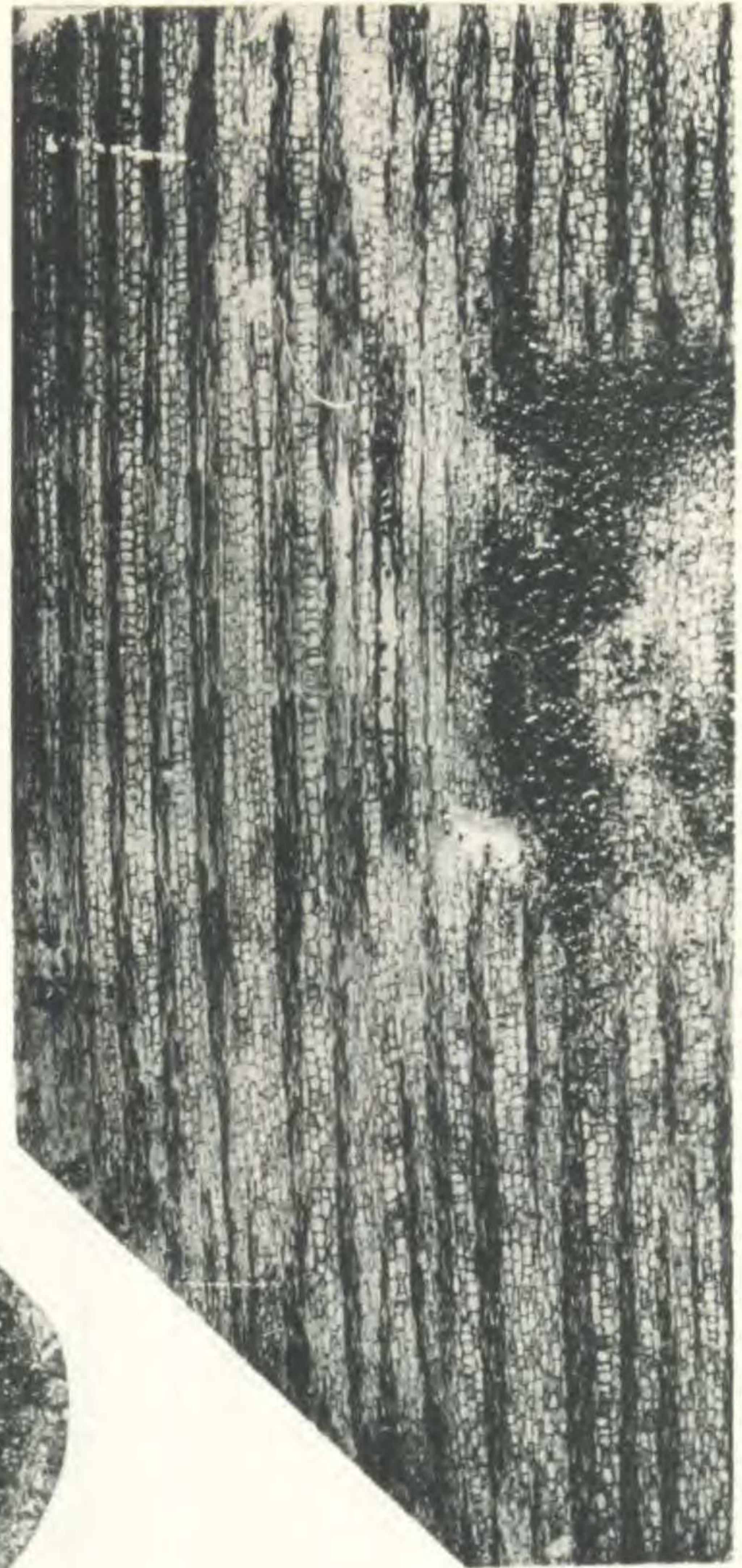
Fig. 20. The outer cortex in transverse section. Slide 1359, x 37.5.

Fig. 21. The outer cortex in tangential section. WCB421-B-S4, x 8.5.

Fig. 22. Leaf trace departing from stele. This is a higher magnification of lt_1 in fig. 17; x 18.5.



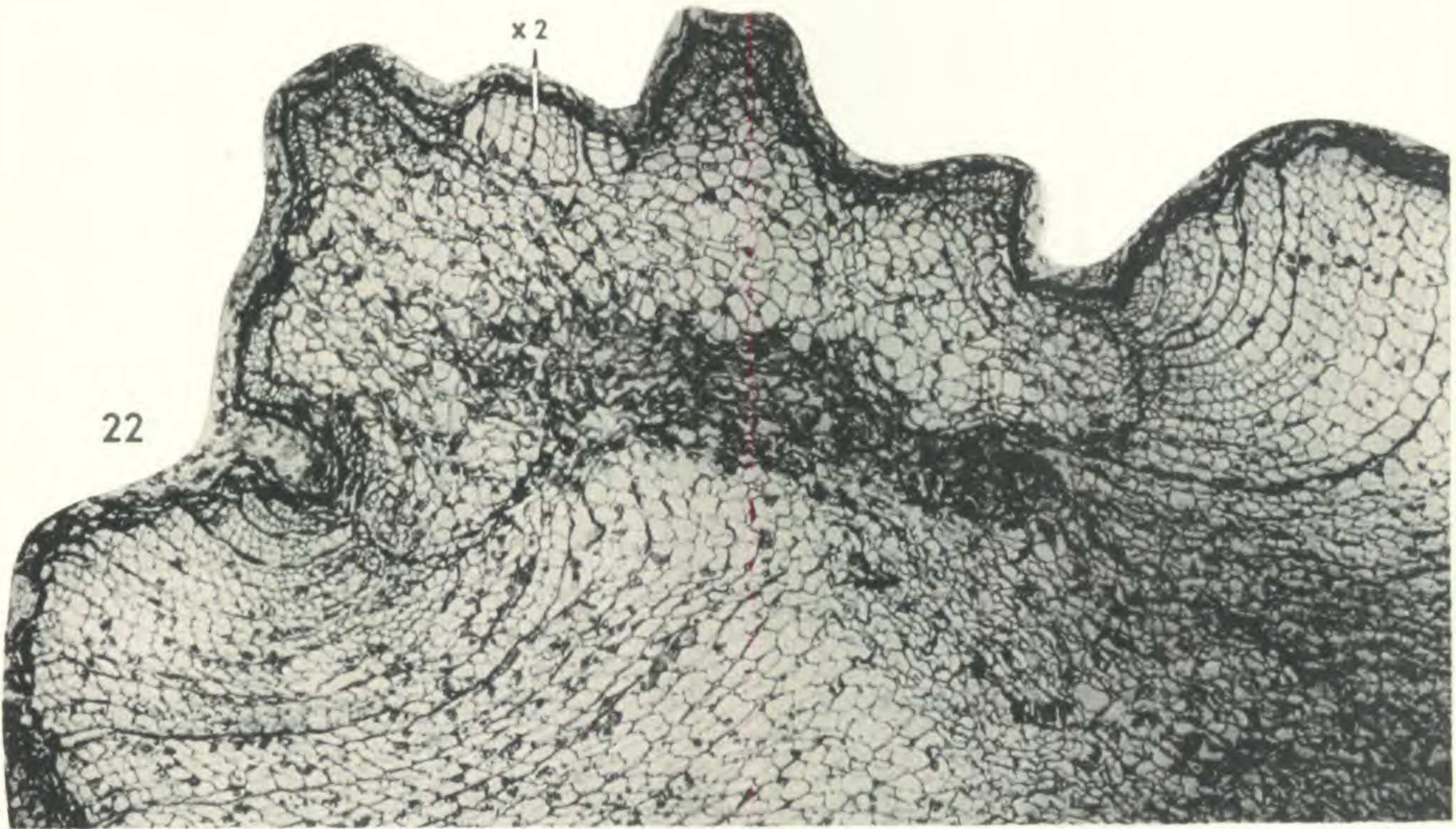
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21



19

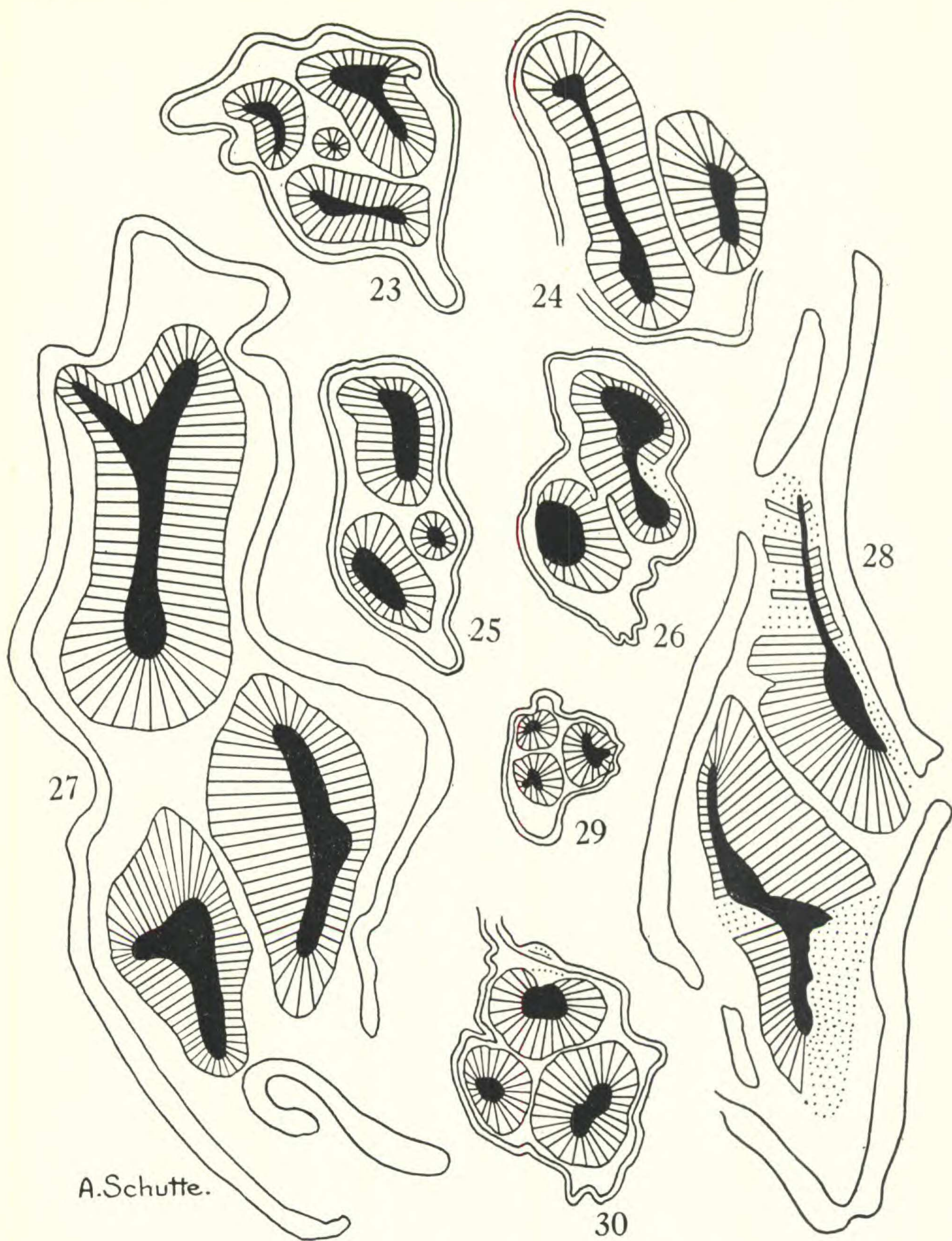


22

EXPLANATION OF PLATE

PLATE 12

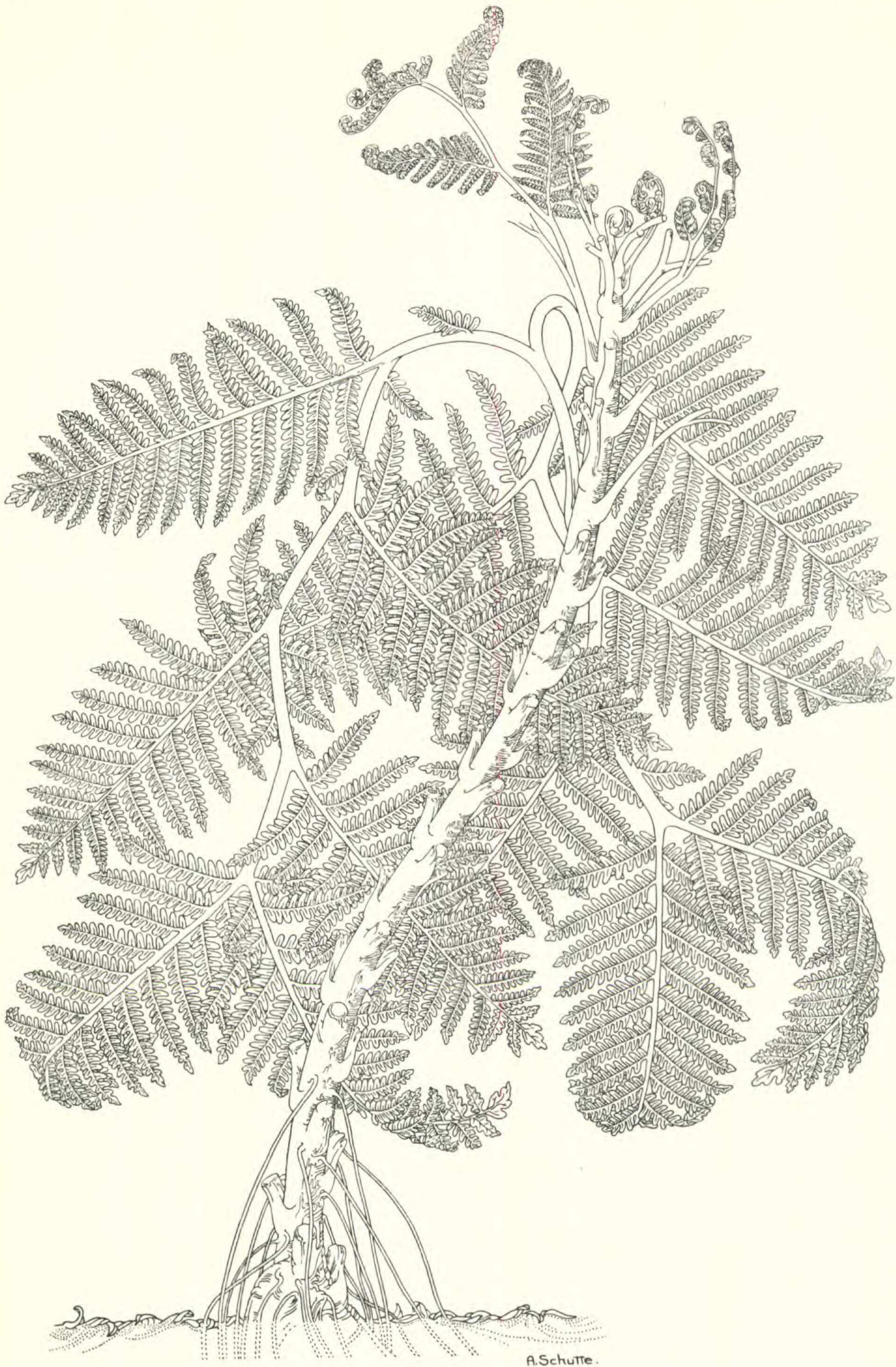
Diagrams of the periderm and stelar systems only of the closely related species of *Medullosa* referable to the sub-genus *Anglorota*. The periderm is indicated by the enclosing, or partially enclosing, double line, the primary xylem in solid black, and the secondary xylem by radiating lines. *The magnification is x 2.8 in all cases.* Fig. 23. *M. centrofilis* De Fraine; fig. 24. *M. sp.* (see page 335); figs. 25, 26. *M. Thompsonii* Andrews; fig. 27. *M. anglica* Scott; fig. 28. *M. distelica* Schopf; fig. 29. *M. pusilla* Scott; fig. 30. *M. anglica* var. *thiessenii* Schopf.



EXPLANATION OF PLATE

PLATE 13

Restoration of a *Medullosa* of the Anglorota group, based primarily on the stem and rachis remains of *M. Thompsonii*, together with associated foliage and root fragments. For further explanation see pp. 332, 334; x approximately 1/8.



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII.

EXPLANATION OF PLATE

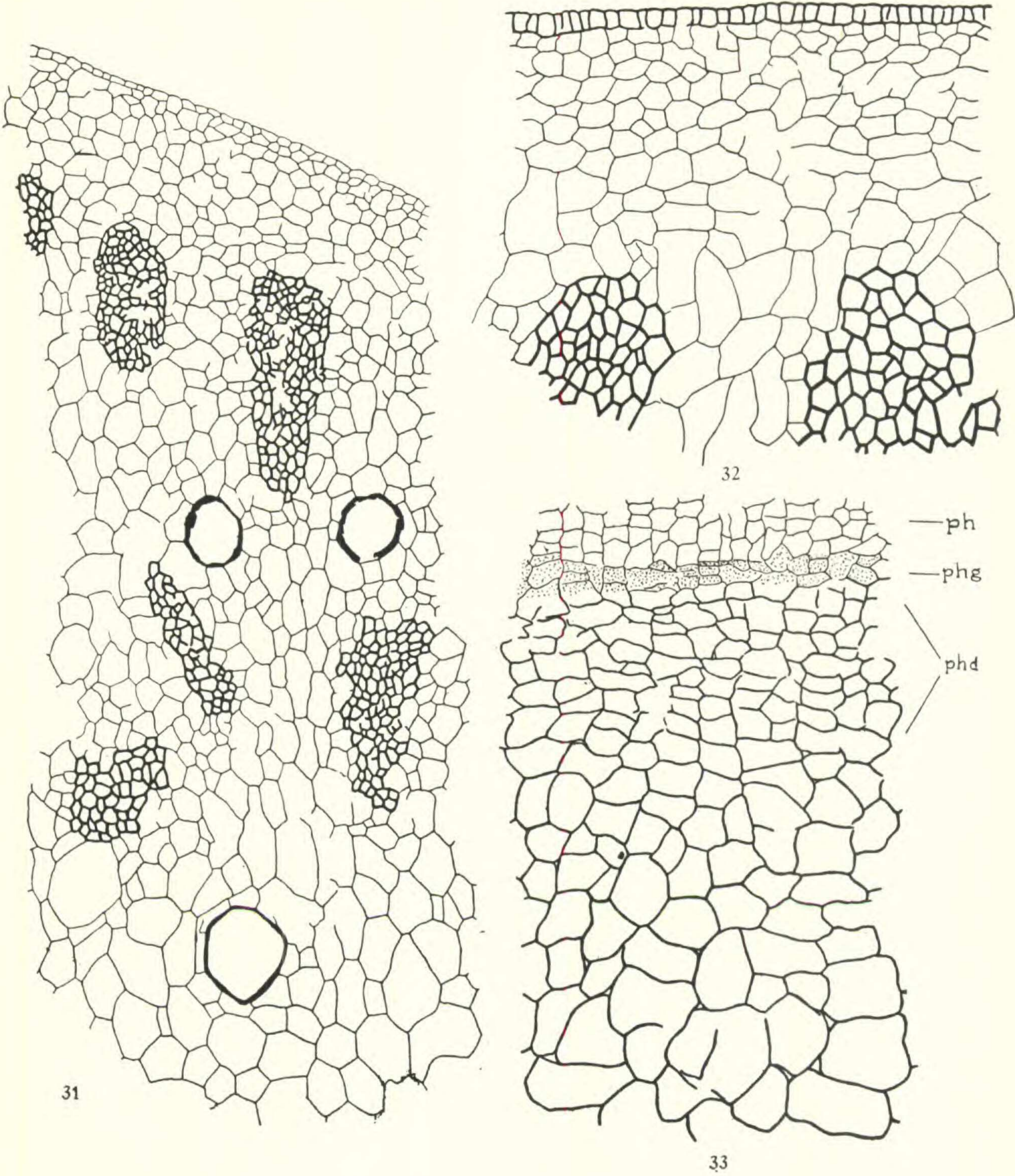
PLATE 14

Medullosa Thompsonii Andrews

Fig. 31. Outer cortex of the petiole shown in fig. 9. WCB426-T2, x 36.

Fig. 32. Outermost cortex and epidermis of the stem shown in fig. 1. A part of two fibrous strands are also shown. Slide No. 1364, x 65.

Fig. 33. Cortex of the stem as it appears between points *b* and *c* of fig. 1: ph, phellem; phg, phellogen; phd, phelloderm. Slide No. 1363, x 65.



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII.

EXPLANATION OF PLATE

PLATE 15

Fig. 34. Reconstruction of *Alethopteris*-like leaflets found associated with the *Medullosa* stems and petioles, x 48. Explanation in text.

Fig. 35. *Myeloxylon Bendixenii*. Outer cortex showing the secretory canals exterior to each fibrous strand. WCB429-S2, x 42.

Fig. 36. *Schopfiastrum decussatum*. Diagram of the transverse section shown in fig. 18. Primary xylem stippled, secondary xylem indicated by radiating lines, and traces solid white; protoxylem groups of primary xylem and traces are shown by large black dots. Slide No. 1353, x 7.5.